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Measuring Stem Growth Rates for Determining Age and Cohort Analysis of a Tropical Evergreen Tree[1]

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ABSTRACT: *Metrosideros polymorpha* (Myrtaceae) is the dominant canopy tree in many Hawaiian lowland and montane rain forests. It is a shade-intolerant species that persists throughout forest succession. Stands usually regenerate following synchronized dieback of the canopy cohort. Like most tropical evergreen trees, *Metrosideros* does not form growth rings, making determination of tree age and stand turnover rates difficult. This study measured the annual stem diameter growth rate for 3 yr in cohorts of six different stem size classes on young volcanic substrates at 1100 m above sea level on the island of Hawai'i. These side-by-side cohorts were assumed to represent a chronosequence of stand development in early primary succession. Growth rates were used to predict mean cohort tree age based on mean tree diameter, adjusting for variation in growth rate during the life cycle of the trees. Mean annual growth rate was about 2 mm yr^{-1} for all the cohorts except the largest, which was significantly lower. This cohort was undergoing stand dieback, with regeneration of a new cohort and is assumed to represent the terminal stage of the cohort life cycle. The predicted age of this cohort was about 200 years; this appears to be a reasonable estimate of the turnover rate for cohorts in this environment. Individual growth rates within cohorts were highly variable. Other parameters, such as crown area and nearest neighbor distances, could not account for the variation. Analysis indicates that the growth rate of each individual tree probably fluctuates about the mean growth rate throughout its life. Year-to-year variation in mean cohort growth rates was significant only for the two largest cohorts. For these large trees, mean growth rate was negatively associated with rainfall. It is suggested that these trees may be light limited, because solar radiation itself is known to be negatively correlated with annual rainfall in the study area.

LIKE MOST TROPICAL, evergreen trees, *Metrosideros polymorpha* Gaud. (Myrtaceae) does not form annual growth rings, making the determination of tree age by standard dendrochronology impossible. Inability to determine age of trees and ignorance of longevity has hampered understanding of forest succession in the highly dynamic Hawaiian lowland and montane rain forest biome, where this species is often the sole canopy tree. *Metrosideros,* like many pioneer tree species, is shade intolerant. Closed forest stands are typically single-generation cohorts of trees with no sapling regeneration beneath the canopy (Jacobi et al. 1983, 1988, Burton and Mueller-Dombois 1984). Cohorts can become established within decades on new volcanic substrates (Atkinson 1970, Drake and Mueller-Dombois 1993). Later, these forests often exhibit stand-level dieback, breaking down in response to what appears to be age- or life cycle-dependent loss of vigor (Mueller-Dombois 1985, 1987, Gerrish 1988, 1990, 1993). A pulse of regeneration of *Metrosi-*

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deros usually follows opening of the canopy, leading to another single-generation cohort, itself subject to eventual stand-level dieback (Stemmermann 1983, Jacobi et al. 1988). It is also known that on some sites, mixed-age stands develop as a result of susceptibility to windthrow and subsequent gap formation (Drake and Mueller-Dombois 1993). *Metrosideros* has persisted as a dominant species through millions of years of forest succession in Hawai'i (Mueller-Dombois et al. 1981).

These cohort dynamics of Hawaiian *Metrosideros* forests are in contrast with the well-documented gap-phase regeneration pattern (Hartshorn 1978) typical of most tropical rain forests, both mixed and single-dominant, the latter of which occur in all tropical regions, often associated with extreme soil conditions (Richards 1996). Cohort dynamics are reported in mixed-species forests of *Aruacaria* on Lord Howe Island (Mueller-Dombois and Fosberg 1998) and in New Guinea (Enright 1993), but are probably more common in island forests with single-dominant forests, such as *Nothofagus* and *Metrosideros* in New Zealand (Ogden et al. 1993) and *Scalesia* (Asteraceae) in the Galápagos (Mueller-Dombois and Fosberg 1998). In some of these examples, poorly developed soils and water regimes of early succession, as well as the disharmonic and depauparate flora typical of remote islands, add further instability, predisposing forests to synchronized canopy dieback.

In Hawai'i, ecosystem process rates are influenced by the cohort dynamics of *Metrosideros*. Productivity, decomposition, and mineralization rates may never reach equilibrium or even a state of gradual, constant change. Nutrient flow processes may fluctuate periodically as the standing-crop biomass of the canopy cohort collapses and then regenerates. Cohort dieback and regeneration has a successional component of directional change as both the genetic makeup of the *Metrosideros* cohort and site factors change. Hawaiian *Metrosideros* stands that regenerate following dieback are sometimes composed of a different genetic ecotype than the previous cohort or a different proportion of two or more ecotypes (Stemmermann 1983, Wagner et al. 1990). It appears that there is a number of ecotypes, with adaptations to conditions ranging from excessively drained to waterlogged soils. Soils and drainage regimes change during primary succession, within the life span of a *Metrosideros* cohort.

The primary objective of this study was to determine the life span of the trees that make up *Metrosideros* cohorts and the turnover rate of the cohorts by developing a model of tree age as a function of stem diameter based on measured growth rates. To determine how stem growth varies during the tree life cycle, we measured the diameter growth rate of *Metrosideros* in cohort stands ranging in tree size from saplings to trees as large as *Metrosideros* grows within the study area environment. This largest-diameter cohort is within a mature stand with more than 50% of the canopy trees dead or dying and with "moderately advanced" regeneration of a new sapling cohort (Mueller-Dombois et al. 1980). These "side-by-side" cohorts are used to represent the chronosequence of growth and development of a single cohort from saplings to stand dieback.

We also analyzed the variation of growth rates within each cohort and the variation between the 3 yr of the study to improve the understanding and model of size versus age. We do not assume that variation in the size of individual trees within a cohort is correlated with tree age; this size : age model should be applied only to cohorts, not individual trees.

In addition to the increase of tree size, the biota and the soil both develop along the chronosequence during the lifetime of a single *Metrosideros* cohort. These environmental changes may affect the growth rate of *Metrosideros*; rather than confounding the analysis of growth rates, these successional developments are the essential context for a size : age model to be used under natural conditions to estimate cohort age.

MATERIALS AND METHODS

The study area is on Kīlauea Volcano in Hawai'i Volcanoes National Park, island of

Hawai'i. The sample cohorts are all within a radius of 1.2 km and between 1100 and 1140 m above sea level. Median annual rainfall is between 2000 and 3000 mm (DLNR 1986); the mean annual rainfall at the nearest rain gauge is 2733 mm. The soils are mapped as Puhimau silt loam, a well-drained Dystrandept formed from volcanic ash and pumice averaging 25 to 40 cm thick over pāhoehoe lava (Sato et al. 1973). The vegetation is 'Ōhi'a/Hāpu'u (*Metrosideros/Cibotium*) Tree Fern Forest (Gagné and Cuddihy 1990) in various stages of successional development. Early successional, open-canopy stands have extensive mats of *Dicranopteris linearis* (Pteridophyta: Gleicheniaceae) and relatively few of the tree ferns *Cibotium* spp. (Pteridophyta: Dicksoniaceae). The reverse is true of the closed stands, where *Cibotium* may form a closed understory canopy. The dominant form of *Metrosideros* within the study area is a form with pubescent leaves, identified as *Metrosideros polymorpha* var. *incana* (Dawson and Stemmermann 1990), and all of the trees measured in this study are of this form.

Six cohorts representing a chronosequence of early primary succession were selected. In each cohort, 10 (11 in one cohort, 12 in one other) dominant trees with good canopy position and as near as possible to the cohort's mean tree diameter at breast height (dbh) were selected for growth measurement. The "current annual growth rate" (defined as dbh increment within one calendar year) of each tree was measured from 1986 to 1988 using band dendrometers. Trees in the sapling cohort were too small to be fitted with dendrometers. Instead, a caliper micrometer was used to measure stem diameter at a point 20 cm above the ground. "Mean annual growth rates" are the averages of each cohort's three current annual growth rates. Thus, data gathered during this study include six paired data points consisting of the initial stem diameter and the mean annual growth rate of each cohort.

These six data pairs were used in an "iterative interpolation" model predicting cohort age as a function of mean tree diameter. A size : age curve was calculated by adding a yearly growth increment to a running diameter, beginning with the mean diameter (D_1) of the cohort of smallest trees (cohort Z). In year 1 the mean annual growth rate (R_1) of the smallest cohort was added to the mean diameter of that cohort, yielding a diameter for year 2 (D_2) (i.e., $D_2 = D_1 + R_1$).

The growth increment for each successive year was calculated by linear interpolation between the six measured data points. This procedure was repeated until the running diameter reached that of the largest diameter cohort. The result of this process is a list of paired ages and diameters spanning the range of initial diameters between the cohorts of smallest and largest trees. These data points were plotted to yield a curve of predicted cohort age as a function of mean tree diameter.

A 95% confidence belt was generated about the mean predicted cohort age. The upper and lower confidence limits were calculated by substituting the upper and lower confidence limits for each mean annual growth rate in the iterative interpolation model. The 95% confidence limits for the cohort mean annual growth rates (and other parameters) were computed as mean $\pm t_{05[n-1]}\ s/\text{sqrt}\ n$, where s = the sample standard deviation and n = number of trees in sample (Sokal and Rohlf 1969).

It was estimated that the sapling cohort (cohort Z) was 13 yr old at the beginning of this study. This estimate is based on the mean height (2.6 m) being 13 times 20 cm, an estimated annual height growth rate for a juvenile tree (Gerrish 1989). Thirteen years were added to the estimated ages of all cohorts to reflect the initial age of the smallest diameter cohort.

Monthly rainfall data for the study period were obtained for the rain gauge at Hawai'i Volcanoes National Park Headquarters (NOAA 1986, 1987, 1988). This rain gauge is 1225 m above sea level and approximately 4 km northwest of the center of the study area. The rainfall data were examined to determine the possible effect of climatic anomalies on tree growth rates during the study period.

Height, crown area, and distance to two nearest neighbor trees were also recorded for

TABLE 1

SAMPLE SIZE (n), MEAN (MEAN), STANDARD DEVIATION (STD), AND COEFFICIENT OF VARIATION (CV) OF INITIAL STEM DIAMETER (DIAM), AVERAGE YEARLY AND MEAN DIAMETER GROWTH RATE FOR EACH COHORT; 95% CONFIDENCE INTERVAL (CI ±) FOR DIAMETER GROWTH RATES; AND THE PREDICTED AGE (AGE) OF EACH COHORT

				DIAMETER GROWTH				
COHORT	n		DIAM (cm)	1986 (mm)	1987 (mm)	1988 (mm)	MEAN (mm)	AGE (yr)
Z	10	Mean	2.43	2.35	1.87	1.86	2.14	13
		STD	0.607	1.30	0.79	0.64	0.86	
		CI ±		0.93	0.57	0.46	0.62	
		CV	25.3				40.2	
A	10	Mean	5.83	2.24	2.03	2.38	2.22	29
		STD	0.440	1.44	1.02	1.35	1.17	
		CI ±		1.03	0.73	0.97	0.84	
		CV	7.7				52.3	
B	11	Mean	9.44	2.20	1.98	1.73	1.97	46
		STD	1.472	0.99	0.73	1.07	0.72	
		CI ±		0.71	0.52	0.76	0.52	
		CV	8.2				36.5	
C	10	Mean	21.13	2.05	1.93	2.40	2.13	101
		STD	1.515	1.06	1.00	1.59	1.14	
		CI ±		0.76	0.72	1.14	0.82	
		CV	7.2				53.5	
D	10	Mean	26.71	1.39	1.96	2.76	2.04	130
		STD	2.061	0.64	0.90	1.21	0.81	
		CI ±		0.46	0.64	0.86	0.58	
		CV	7.7				39.7	
E	12	Mean	36.84	0.72	1.02	1.58	1.11	195
		STD	0.45	0.65	0.88	0.80	0.72	
		CI ±		0.46	0.63	0.57	0.52	
		CV	11.0				64.9	

each tree at the beginning of the study. These parameters and the annual increments for the 63 individual trees are given in the Appendix.

RESULTS AND DISCUSSION

Measured Growth Rates and Predicted Cohort Turnover Time

Metrosideros polymorpha was found to be relatively slow growing at these study sites, averaging about 2 mm annual diameter increment (Table 1). The mean annual growth rates of all the cohorts were surprisingly uniform (Figure 1). It had been expected that the annual growth rate would vary as a modal curve through the chronosequence, as has been found with *Acacia koa* Gray (Fabaceae), another dominant tree in some Hawaiian rain forests (Mueller-Dombois et al. 1981:271). The mean annual stem diameter growth rate of *A. koa* is at its greatest, 20 mm yr^{-1}, in medium-sized trees 25 cm in diameter.

Only the largest diameter trees (cohort E) grew significantly slower than the other cohorts (Table 2). The implication of this decline in the growth rate of large trees is made clear by converting diameter growth to total stem biomass increase using an allometric relationship established for *Metrosideros polymorpha* in a nearby, environmentally similar site (Gerrish 1990):

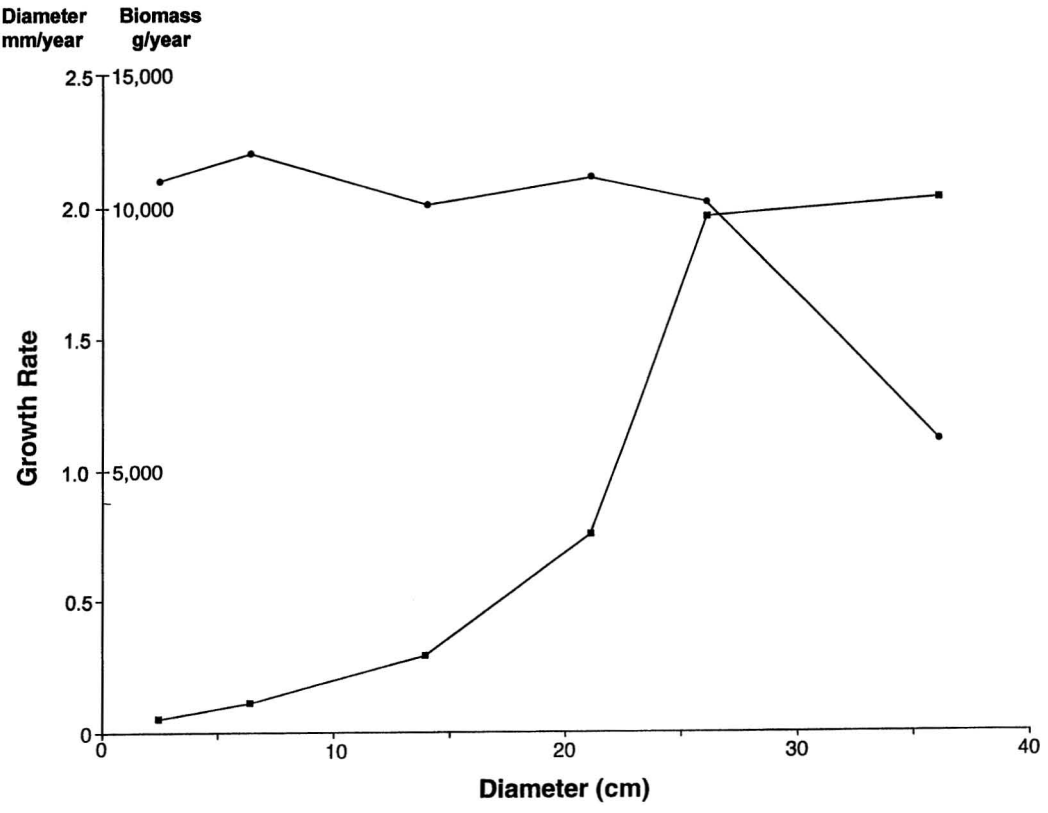

FIGURE 1. Mean annual diameter (circles) and stem biomass (squares) growth rates of six *Metrosideros* cohorts.

$$\log(\text{stem volume}) = 2.96 \log(\text{stem diameter}) + 1.54,$$

and using 0.75 g cm^{-3} as the dry-weight density of the wood (unpubl. data). Stem biomass (volume) increases exponentially through most of the chronosequence before becoming linear at a stem size greater than 27 cm (Figure 1). Apparently exponential biomass increase is the normal condition for vigorous *Metrosideros polymorpha* trees. Decline in the diameter growth rate and the end of exponential growth may signal the onset of senescence, a life state in which growth and maintenance are restricted by insufficient photosynthate (Gerrish 1990) or other internal causes. The decline in biomass production after a species-specific age is well known to foresters, but is usually given on a per-stand rather than a per-tree basis (Smith 1962).

Similar growth rates have been reported from other studies of *Metrosideros*. On a nearby site where some canopy dieback had previously occurred, mature trees showing at least 10% canopy defoliation within a cohort averaged approximately 0.8 mm ($\pm$0.17 standard error, coefficient of variation 84%) annual diameter growth over 26 months. At two other more distant montane rain forest sites, trees in similar conditions averaged approximately 0.9 mm ($\pm$0.25, coefficient of variation 92%) annual growth. In all three of these stands, however, the growth rates of the individual trees varied by a factor of 10 (Gerrish et al. 1984). At another nearby, early succession site trees 3 to 7 m tall, growing in recent volcanic cinder, grew 1.1 $\pm$ 0.2 mm/yr (Walker and Vitousek 1991). In New Zealand, diameter growth rates of *Metrosideros umbellata* greater than

TABLE 2

A. ANALYSIS OF VARIANCE OF MEAN ANNUAL COHORT GROWTH RATES (MM YR^{-1}) FOR THE EFFECT OF "COHORT" AND "YEAR." B. FISHER'S MEANS TEST: COHORT MEANS INDICATED WITH SAME LETTER (DIFF) ARE NOT SIGNIFICANTLY DIFFERENT (95% CONFIDENCE LEVEL)

A.

Source of Variation	df	ms	*F*	*P*
Year	2	0.01828	1.7	0.186
Cohort	5	0.05677	5.27	<0.001
Year × Cohort	10	0.01412	1.31	0.229
Error	166	0.01077		

B.

COHORT	MEAN	DIFF
Z	2.14	A
A	2.22	A
B	1.97	A
C	2.13	A
D	2.04	A
E	1.11	B

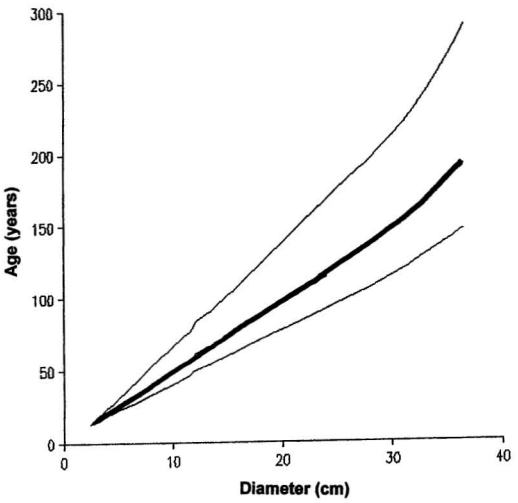

FIGURE 2. Relationship between predicted age and stem diameter (heavy line) with 95% confidence belt based on growth rates of *Metrosideros*.

7.5 cm basal diameter were found to be no more than 2.0 mm/yr throughout its altitudinal range (Payton 1989).

The cohort mean annual growth rates were used in the iterative interpolation model to generate a graph predicting cohort age as a function of mean tree diameter with a confidence belt around the age estimate (Figure 2). The estimated age of cohort E, the cohort undergoing dieback, is 195 yr.

The near uniformity of mean annual cohort growth rates in Hawaiian *Metrosideros polymorpha* allows mean stem diameter to be used directly as a linear correlate with cohort age, until late in the chronosequence when the tree growth rate declines. An age of 191 yr could be estimated for cohort E by dividing the mean diameter by 1.93 mm, the average of all six cohort mean annual growth rates. These estimates of the age for cohort E conform with the known age of the underlying volcanic substrate erupted in the year 1790, 196 yr from the beginning of this study (Wolf and Morris 1996; J. Lockwood, U.S. Geological Survey, pers. comm.). Invasion of new ash substrates by *Metrosideros polymorpha* within several years of eruption has been documented on Kīlauea (Smathers and Mueller-Dombois 1974). Thus, approximately 200 yr appears to be a reasonable estimate of the cohort turnover time in this environment.

Although the mean growth rates of five of the six cohorts were nearly uniform, there was high tree-to-tree variation within each cohort, resulting in a 95% confidence belt for the predicted age that becomes wider with increasing tree size and age (Figure 2). The belt is asymmetrical, showing a greater likelihood that the model would underestimate rather than overestimate cohort age (e.g., predicted age of a cohort with mean dominant tree diameter of 36 cm is 192 yr; using the lower and upper growth rate confidence limits [Table 1] predicts, respectively, 290 yr [51% above mean] and 147 yr [23% below mean]).

Explaining Tree-to-Tree Variation

The discovery of a wide tree-to-tree variation in growth rates raises important questions for stand development analysis. The coefficient of variation (CV) of each cohort's mean annual growth rate is much greater than the CV of mean tree diameter within the cohort (Table 1). This tree-to-tree variation is

TABLE 3

CORRELATION (r) OF YEARLY TREE GROWTH BETWEEN YEARS FOR THE SIX COHORTS

	1986 × 1987	1987 × 1988	1986 × 1988
COHORT	r	r	r
Z	0.64	0.44	0.60
A	0.73*	0.78*	0.75*
B	0.57	0.45	0.30
C	0.83*	0.75*	0.88*
D	0.59	0.85*	0.50
E	0.76*	0.92*	0.68*

* r significantly different from zero at 95% confidence level.

poorly correlated with tree diameter, height, crown diameter, and a competition index (data in Appendix, multiple regression analysis unpubl.) and, thus, these tree and stand attributes cannot be used to improve the size : age model.

How can the trees within each cohort sample, assumed to be the same age, have reached the same diameter when they exhibit annual growth rates that differ by a factor of three or four (Appendix)? Although this question may not be resolved here, several reasonable alternative hypotheses are evaluated below.

ALTERNATIVE HYPOTHESIS 1. The six sample cohorts are not even-aged, but momentary collections of same-sized trees. The stands are made up of consistently fast- and consistently slow-growing trees. Inspection of the individual tree data (Appendix) and correlation analyses (Table 3) do show that annual growth rate is a fair predictor of the following year's growth rate and of growth in 2 yr (i.e., 1986 growth as a predictor of 1987 and 1988 growth).

However, this hypothesis requires that the fast-growing trees all be much younger than the slow-growing trees. The age of the trees within each cohort would differ by a factor between three and eight, if estimated by dividing the mean cohort diameter by the annual growth rates of the fastest-growing and the slowest-growing tree of each cohort. This hypothesis can be refuted, at least for the trees of cohort E, by considering that the volcanic substrate of that site is known to be about 200 yr old. A tree of the mean cohort diameter, 36.8 cm, would not have reached this size in that time span by consistently growing at the rate of the slowest tree of each cohort or at the lower 95% confidence limit.

ALTERNATIVE HYPOTHESIS 2. Stands are even-aged cohorts that have grown together at relatively uniform rates, but the growth rates of some trees have recently declined. These lower growth rates are an indication of declining vigor. Although all sample trees in this study were chosen for vigorous appearance, the now slow-growing trees may be becoming suppressed and could be eliminated by stand self-thinning, which constantly occurs during cohort development. Self-thinning of establishing stands, from seedling to pole stage, has been previously documented in *Metrosideros polymorpha* (Jacobi et al. 1983, 1988).

Observations during a return visit to the study sites in 1997 give little support for this hypothesis. All of the trees of cohorts A, C, D, and E were revisited. Five of the trees of cohort B were relocated; the site of cohort Z was not revisited. The vigor of each tree was assessed by estimating the percentage of defoliated branches in the upper crown. None of the revisited trees of cohorts A, B, C, or D showed more than very minor defoliation; none appeared to be declining in vigor. Only in cohort E was any defoliation and change in vigor apparent, revealing a weak association between current vigor and the growth rate measured 9 yr earlier (Table 4). The two slowest-growing trees showed substantial loss of vigor; the first of these was in obvious decline, with the highest branches completely dead. Other than these two trees, however, the association within the cohort is inconsistent ($r = 0.458$, $P = 0.134$). It appears that slow growth may indicate approaching defoliation and loss of vigor in mature trees, but not generally in younger trees.

ALTERNATIVE HYPOTHESIS 3. Stands are even-aged and over the long term trees are growing at approximately uniform rates, not consistently fast or slow. Growth rates of individual trees vary over time, not in response

TABLE 4

MEAN GROWTH RATE FROM 1986 TO 1988 AND THE PERCENTAGE DEFOLIATION OF THE UPPER CANOPY OF TREES OF COHORT E IN 1997

TREE	MEAN GROWTH	% 1997 DEFOLIATION
E7	0.03	20
E12	0.04	15
E6	0.05	0
E8	0.06	0
E10	0.06	5
E5	0.07	15
E9	0.09	0
E1	0.14	15
E2	0.17	0
E4	0.17	5
E11	0.20	0
E3	0.25	0

to suppression or specific climatic factors, but as part of a highly plastic growth pattern, not easily understood in a short-term (3 yr) time frame.

Explaining Year-to-Year Variation

The current annual growth rates vary significantly only within cohorts D and E, the larger trees (Table 5). The patterns of year-to-year variation in these two cohorts are the same, with growth in 1988 being significantly higher than in the other 2 yr. The growth rates are negatively correlated with the annual rainfall, which was 307 cm in 1986, 250 cm in 1987, and 224 cm in 1988. The correlation is not statistically significant. Growth of these large trees may be light limited and associated with solar radiation (Gerrish 1990, 1993). In the vicinity of the study area, solar radiation has been reported to be negatively correlated ($r^2 = 0.92$) with rainfall (Yoshihara and Ekern 1977). The lack of association between mean annual growth rate and annual rainfall in the four other cohorts may imply that growth was not limited by annual rainfall or any other directly associated climatic factor.

CONCLUSIONS

Metrosideros polymorpha is a slow-growing, long-lived tree of about 200 yr or more. The relative uniformity of mean growth rates (about 2 mm yr^{-1}) found in the study environment simplifies aging cohorts, except among larger trees that exhibit lower growth rates. However, high tree-to-tree variation may result in wide ranges of stem diameters within stands, especially in cohorts of larger trees.

Available data best support the model of even-aged cohorts, but raise questions about individual tree growth performance during stand development.

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TABLE 5

ONE-WAY ANALYSES OF VARIANCE AND FISHER'S MEANS TEST COMPARING ANNUAL GROWTH BETWEEN THE 3 YR OF STUDY FOR EACH OF THE TWO COHORTS WHERE DIFFERENCES ARE SIGNIFICANT

	SOURCE	df	ms	F	$P > F$	YEAR	MEAN	DIFF
Cohort D	Year	2	0.047	5.30	0.01	1986	1.39	A
	Error	27	0.009			1987	1.96	A
						1988	2.76	B
Cohort E	Year	2	0.023	3.74	0.03	1986	0.73	A
	Error	33	0.006			1987	1.02	A
						1988	1.58	B

df, degrees of freedom; ms, mean square; F, value of F statistic; $P > F$, probability that differences between all means are due to chance; DIFF, results of Fisher's Means Test: means indicated with same letter are not significantly different at 95% confidence level.

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APPENDIX

INITIAL STEM DIAMETER (DIAM), HEIGHT (HGT), CROWN OUTLINE AREA (CROWN), COMPETITION INDEX (COMP IND), CURRENT ANNUAL STEM DIAMETER GROWTH (1986, 1987, 1988), AND MEAN OF THE 3 YR OF DIAMETER GROWTH (MEAN) FOR THE INDIVIDUAL TREES USED IN THIS STUDY

TREE NO.	DIAM (cm)	HGT (m)	CROWN (m^2)	COMP IND	DIAMETER GROWTH (mm)			
					1986	1987	1988	MEAN
Z1	2.9	2.9	0.16	94.0	0.9	1.0	1.6	1.17
Z2	1.6	1.7	0.11	8.8	2.1	1.0	1.9	1.67
Z3	2.3	1.9	0.24	8.7	4.8	2.3	*	3.55
Z4	1.8	2.2	0.13	31.2	1.7	1.6	1.7	1.67
Z5	2.8	3.2	0.33	17.5	3.4	3.0	1.4	2.60
Z6	3.0	2.6	0.38	37.0	3.2	*	2.8	3.00
Z7	2.2	2.7	0.20	30.7	3	2.0	*	2.50
Z8	1.7	2.3	0.10	14.3	1	1.1	1.0	1.03
Z9	2.8	3.1	0.49	28.1	0.8	2.0	*	1.40
Z10	3.4	3.6	0.71	21.3	2.9	3.0	2.6	2.83
A1	6.6	5.7	1.23	40.7	4.9	3.5	4.4	4.27
A2	5.2	5.5	1.13	35.7	2	2.1	1.6	1.90
A3	6.1	5.3	0.71	18.4	2.4	1.3	2.3	2.00
A4	6.9	6.4	0.75	97.3	1.6	0.5	2.3	1.47
A5	6.2	6.3	1.13	8.0	4.4	3.6	4.6	4.20
A6	6.3	5.2	1.12	13.2	2.1	2.3	1.7	2.03
A7	6.4	5.7	0.94	60.4	0.6	1.0	0.7	0.77
A8	6.6	5.7	0.78	7.5	2.5	1.6	1.1	1.73
A9	6.3	6.2	1.32	18.3	1.4	2.7	3.5	2.53
A10	6.9	6.3	1.21	13.7	0.5	1.7	1.7	1.30
B1	13.4	8.8	11.00	156.2	1.7	1.6	*	1.65
B2	14.6	10	13.37	22.9	1.9	1.4	2.1	1.80
B3	14.9	8.4	13.19	20.9	1.5	2.3	2.0	1.93
B4	12.4	9.2	6.57	814.4	3.9	3.1	4.1	3.70
B5	12.3	8.5	4.29	10.9	4.1	2.6	1.3	2.67
B6	14.4	7.8	10.80	27.2	2.6	2.7	0.8	2.03
B7	14.2	12	4.52	47.2	1.6	2.6	2.5	2.23
B8	14.9	8.5	4.92	155.1	1.1	1.0	0.9	1.00
B9	12.1	8.1	6.60	139.4	1.4	1.6	2.0	1.67
B10	15.0	11.3	5.65	1,482.9	1.9	2.0	0.4	1.43
B11	13.2	11.3	5.50	3,438.3	2.5	0.9	1.2	1.53
C1	19.0	11	9.11	18.6	2.6	1.9	2.7	2.40
C2	22.4	12.5	14.40	20.5	2.1	2.0	1.2	1.77
C3	23.0	12.3	16.10	31.5	2	2.1	1.6	1.90
C4	19.4	11.6	21.99	157.6	0.5	0.1	0.5	0.37
C5	22.8	12.7	26.01	35.9	2.1	1.1	0.9	1.37
C6	21.3	15.5	11.55	43.5	1	1.1	1.9	1.33
C7	21.4	14.2	27.89	1,090.8	1.8	2.4	3.1	2.43
C8	19.0	14.3	10.37	72.0	2.3	2.3	2.5	2.37
C9	21.1	14.6	12.64	88.6	4.5	3.8	5.9	4.73
C10	21.9	9.5	11.62	23.3	1.6	2.5	3.7	2.60
D1	27.7	17.3	20.40	58.5	1.5	1.5	2.1	1.70
D2	24.7	16.2	12.21	46.6	2.3	3.0	3.4	2.90
D3	29.2	17.7	29.25	133.1	1.6	1.0	1.2	1.27
D4	25.1	17	20.23	155.9	0.2	0.8	1.9	0.97
D5	25.5	15.6	17.01	157.6	1.3	2.8	3.6	2.57
D6	24.2	15.6	11.91	177.4	1	2.5	2.4	1.97
D7	28.2	16	20.45	1,979.2	2.2	3.0	4.4	3.20
D8	27.3	19.8	9.34	162.7	1.4	2.6	4.7	2.90
D9	25.1	18.4	16.56	50.2	0.7	1.1	1.4	1.07
D10	30.1	16.5	23.37	157.6	1.7	1.3	2.5	1.83

APPENDIX (continued)

TREE NO.	DIAM (cm)	HGT (m)	CROWN (m^2)	COMP IND	DIAMETER GROWTH (mm)			
					1986	1987	1988	MEAN
E1	38.5	16.5	42.98	95.5	0.9	1.2	2.0	1.37
E2	33.9	17	29.22	59.0	0.9	1.7	2.5	1.70
E3	33.4	20.5	9.74	976.0	2.4	2.3	2.7	2.47
E4	33.8	17.3	13.15	119.0	0.5	2.0	2.7	1.73
E5	33.7	16.5	38.48	366.2	0.3	0.7	1.0	0.67
E6	36.8	21.3	35.22	123.9	0.1	0.2	1.1	0.47
E7	37.4	17	18.86	40.4	0.2	0.2	0.6	0.33
E8	35.5	18.2	18.66	71.8	0.2	0.3	1.3	0.60
E9	32.5	20.3	12.88	110.3	0.7	0.9	1.1	0.90
E10	38.2	18.4	41.94	70.8	0.7	0.1	1.1	0.63
E11	46.0	23.5	38.99	209.3	1.4	2.4	2.3	2.03
E12	42.4	19.5	21.10	337.0	0.4	0.2	0.6	0.40

COMP IND, Basal area of nearest neighbor divided by square of distance to nearest neighbor plus basal area of second nearest neighbor divided by square of distance to second nearest neighbor.

* Missing value.